Copeia, 2006(4), pp. 604–612

Seasonal Feeding Specialization on Snails by River Darters (*Percina shumardi*) with a Review of Snail Feeding by Other Darter Species

WENDELL R. HAAG AND MELVIN L. WARREN, JR.

We report food habits of River Darters (*Percina shumardi*) in Brushy Creek and the Sipsey Fork Black Warrior River, Alabama. River Darters preyed heavily on pleurocerid snails in both streams. Snail feeding varied widely among sample dates and was highest in October when snails represented nearly 100% of darter food items. Snail feeding declined through the spring, nearly ceasing by May, but increased to high levels again in July when hatchling snails composed about 80% of darter food items. Mean and maximum size of snails eaten increased with darter size, but minimum snail size was not related to darter size, indicating a broadening of prey size for larger darters. Non-snail food items were dominated by chironomid, trichopteran, and ephemeropteran insect larvae; these food items were most commonly eaten during periods of low snail feeding or feeding on hatchling snails. Specialization for snail feeding is suggested for all species in the subgenus *Imostoma*, including *P. shumardi*, but this feeding habit is well documented previously only for *P. tanasi*. Published diet studies for other species of *Imostoma*, including populations of *P. shumardi* from elsewhere in its range, did not document snail feeding; most other observations of snail feeding for the group are anecdotal. Few other darters or other fish species are documented to prey heavily on riverine snails. Although the limited amount of published information makes it difficult to assess the degree to which *Imostoma* as a group relies on snails as a food source, *P. shumardi* and *P. tanasi* represent two of the few native fishes that exploit the abundant and diverse pleurocerid snail fauna of eastern North America.

DARTERS (Percidae: Etheostomatinae) are a diverse group of small benthic fishes that feed mostly on aquatic insect larvae or other small aquatic arthropods (Page, 1983). The most notable deviation from this generalized feeding pattern is the heavy use of pleurocerid snails reported for species in the subgenus *Imostoma* (genus *Percina*). *Imostoma* is a monophyletic clade consisting of *Percina antesella, P. shumardi, P. tanasi, P. uranidea*, and *P. vigil* (Page, 1974a; Near, 2002). Feeding specialization on snails is suggested for all species of *Imostoma* (Etnier and Starnes, 1993) but is documented well only for *P. tanasi* (Starnes, 1977). The rarity or sporadic occurrence of most species of *Imostoma*, coupled with their preference for deep, swift riffles in small to large rivers (Page and Burr, 1991), makes it difficult to obtain large numbers of individuals on a regular basis (Thomas, 1970; Sanders and Yoder, 1989); consequently, food habits of this group of fishes are poorly known. We report food habitats of the River Darter, *P. shumardi*, from two populations in the upper Black Warrior drainage in Alabama. We also analyze seasonal and ontogenetic variation in snail feeding by River Darters and review available information on snail feeding in *Imostoma* and other darter species.

MATERIALS AND METHODS

Sampling sites and collections.—We collected River Darters at one site each on the Sipsey Fork Black Warrior River (order VI, 34°15′10″N, 87°22′02″W) and Brushy Creek (order V, 34°13′11″N, 87°14′49″W) in Winston County, Alabama, within Bankhead National Forest. Stream width was 4–21 m at the Sipsey Fork site (mean = 12) and 3–13 m at the Brushy Creek site (mean = 8); depth at both sites varied from a few cm in riffles to 2 m in pools. Both streams are relatively unmodified by humans and support diverse biological communities (Haag and Warren, 1998) including seasonally abundant populations of River Darters. We sampled fishes by backpack electrofishing (21.9–52.2 min/sample) at both sites intermittently from October 1993 to July 1995. We preserved specimens in 5% buffered formalin and later transferred them to 70% ethanol. We deposited voucher specimens at the University of Alabama Ichthyological Collection (UAIC 14426.01–14434.01).

Diet evaluation.—In the laboratory, we measured standard length (SL, nearest 0.1 mm) and dissected the entire digestive tract of each fish. We did not examine guts of fish collected from the Sipsey Fork in April and August 1995 because specimens were inadvertently misplaced. We washed the contents of each gut into a Petri dish and identified and counted food items under a stereomicroscope. For food items that were incomplete or partially digested (e.g., dipteran larvae), we counted head capsules only. Size distribution of snails found in guts over the course of the study was bimodal due to the appearance of large numbers of hatchling snails in summer. We defined hatchling snails as individuals $\leq$ 1.5-mm maximum length; we refer to snails $>$ 1.5 mm as larger snails. We measured the maximum length and width (nearest 0.1 mm, dial calipers) of all larger snails but did not measure hatchling snails. Length was the distance from the apex of the spire to the anterior edge of the basal lip, and width was the distance across the last body whorl to the outer lip (Burch, 1982).

Data analysis.—We expressed darter abundance on each sample date as catch per unit effort (CPUE, number of fish/min). We tested for differences in darter mean size among streams and sample dates using analysis of variance with inverse square transformation of length (length^{-2}) to achieve normality and homogeneity of variances. For this analysis, we considered samples taken at different sites within six days of each other to be a single date, and we excluded samples for which we did not examine any darter guts. We tested for ontogenetic shifts in snail use by darters in two ways. First, we used linear regression to test for relationships between size of darters and size of ingested snails using the minimum, mean, and maximum size of snails found in each individual fish captured in October, April, and May. We excluded fish captured during periods when hatchling snails were present (June and July) because the occurrence of this distinct size class of small snails confounded attempts to analyze relationships between darter and snail size. Second, we used linear regression to test for relationships between size of darters and numbers of ingested larger snails and hatchling snails separately, using observations only from time periods during which darters were feeding heavily on each respective snail size class (larger snails, October and April; hatchling snails, July). Because of the visual pattern of data scatter for hatchling snails, we tested the relationship of darter size to number of hatchlings ingested using linear regression and shape-and-boundary analyses (10,000 simulations; EcoSim: null models software for ecology. Version 7. N. J. Gotelli and G. L. Entsminger, Acquired Intelligence Inc. and Kesey-Bear, 2001. http://homepages.together.net/ngentsminger/ecosim.htm.). Shape-and-boundary analysis is a randomization technique that can detect non-random patterns in bivariate scatterplots of data.

Review of snail feeding in darters.—We reviewed the literature for accounts of snail feeding by other darter species. For species other than *Imostoma*, we classified the prevalence of snails in darter diets as high or low. We considered snail use by a species to be high when in at least one study snails composed $\geq$25% of food items (by frequency or volume) or when authors qualitatively described snails as a predominant food item. We considered snail use to be low when snails composed $<$25% of food items or when authors qualitatively described snail occurrence as low or incidental. For each species, we cited only papers reporting snail feeding; for most common and widespread species a number of other studies did not report snails as a food item (e.g., *Etheostoma blennioides*).

RESULTS

Darter size and abundance.—We captured 151 River Darters and examined stomachs of 113 specimens (Table 1). Overall River Darter abundance was higher in the Sipsey Fork than in Brushy Creek (Mann-Whitney $U = 25$, $P < 0.05$), but abundance varied widely among sample dates in both streams. Darter mean length did not differ between streams but differed significantly among sample dates ($F_{5,8} = 9.48$, $P < 0.0001$; stream $\times$ date interaction not significant); the largest fish were present in October in both streams (Table 1). Only three fish had empty stomachs (one each in April, May, and June).

Seasonal use of snails.—Snails were a common and conspicuous prey item for River Darters in both streams and constituted over half of all items found in guts across sample dates (Table 2). Guts of large River Darters were often stuffed with snails (Fig. 1). All snails found in guts were referable to *Elimia* sp. (Pleuroceridae). All snails consumed by River Darters were juveniles; the mean size of larger snails consumed was 2.7 mm in width (range = 1.2–4.7) by 4.3 mm in length (range = 1.9–10.4). At the study sites, adult snails reach a maximum size of about 11 mm in width by 24 mm in length (W. Haag and M. Warren, unpubl. data).

Use of snails by River Darters varied widely among sample dates. Relative occurrence of snails in guts was highest in October when snails represented nearly 100% of River Darter food items in both streams (Table 2). Relative occurrence of snails declined from April to June but

TABLE 1. CATCH PER UNIT EFFORT (CPUE) AND SAMPLE SIZE FOR DIET DETERMINATION OF RIVER DARTERS (*Percina shumardi*) IN THE UPPER BLACK WARRIOR RIVER DRAINAGE, ALABAMA. Darter mean length pertains only to specimens for which gut contents were examined.

Stream	Date	Sample time (min.)	CPUE (number of fish · min^{-1})	Darter mean length (mm, range)	Number of specimens examined
Brushy Creek	28 Oct. 1993	41.52	0.05	58.6 (53.7–63.5)	2
	15 April 1994	26.45	0.19	43.4 (41.4–44.7)	5
	14 April 1995	37.37	0.32	47.3 (42.4–53.3)	12
	16 May 1995	26.07	0.19	43.7 (40.5–47.1)	5
Sipsey Fork	28 Oct. 1993	52.18	0.31	55.5 (47.9–66.6)	16
	14 April 1994	26.68	0.30	55.2 (39.0–58.0)	6
	14 April 1995	28.53	0.21	—	0
	10 May 1995	21.93	0.78	42.6 (37.4–55.2)	16
	13 June 1995	37.95	0.95	44.2 (38.0–65.8)	34
	19 July 1995	22.12	0.81	46.4 (38.7–64.7)	17
	15 Aug. 1995	22.52	1.15	—	0

rose again in July when snails represented > 80% of River Darter food items in the Sipsey Fork. The temporal pattern of mean number of snails eaten by River Darters was similar to the pattern of relative occurrence in guts except that mean number of snails in darter guts was about four times higher in July than in October (Table 2). During this summer peak in snail use, snails eaten by River Darters were predominantly hatchlings, and larger snails were eaten only rarely; hatchlings composed 93% of all snails found in guts in July. Similarly, although smaller numbers of hatchling snails were eaten in June, hatchlings composed 99% of total snails ingested. Hatchling snails were not found in River Darter guts at any other time of year. We were not able to evaluate the use of hatchling snails by River Darters in Brushy Creek because June and July samples were unavailable for that stream.

Relationship of darter size to snail size and number.— Mean size and maximum size of snails eaten by darters were related positively to fish length (Mean: snail width = 1.024 + 0.033(darter length), $R^2 = 0.29$, $P < 0.01$; Maximum: snail width = −0.991 + 0.085(darter length), $R^2 = 0.58$, $P < 0.0001$), but minimum size of snails eaten by darters was not related to fish length. Larger snails were preyed upon most heavily by large darters, and small fish ate few or no larger snails (Fig. 2). The largest snail found in guts (10.4 mm in length) was eaten by a 66.6-mm SL fish that had also eaten 13 other snails averaging 6.3 mm in length. Hatchling snails were preyed upon heavily by small darters, but even large fish ate hatchling snails during periods of availability in June and July. There was no significant regression relationship between the number of hatchling snails eaten by fish and fish size, and shape-and-boundary analysis indicated that the observed pattern was not significantly different from random (Fig. 2). During periods of heavy snail feeding, whether on larger snails or hatchlings, most darter stomachs contained snails (Fig. 2).

Other food items.—In addition to snails, River Darters ate a wide variety of other aquatic organisms (Table 2). Non-snail prey items were dominated by midge (Diptera: Chironomidae) and caddisfly (Trichoptera) larvae, and to a lesser extent, mayfly (Ephemeroptera) larvae. All other organisms found in darter guts each constituted less than 1% of total prey items across sample dates. Of interest was the sporadic occurrence in darter guts of cases and larvae of *Helicopsyche* sp., a caddisfly that builds a coiled case of cemented sand grains that closely resembles a small snail. These cases were consumed whole by darters as were non-coiled cases of other caddisfly species. Fish eggs occurred in guts in May and June but were rare with the exception of a single fish in May that had consumed nine eggs. In addition to snails, the only other mollusk found in guts was the Asian clam, *Corbicula fluminea* (mean length = 2.3 mm, range 1.5–4.2, $n = 12$), but it occurred rarely. River Darters ate large numbers of non-snail food items coincident with heavy feeding on hatchling snails. In contrast, during periods of heavy feeding on larger snails, darters ate few other food items.

DISCUSSION

Snails were the predominant food item consumed by River Darters in the Sipsey Fork and Brushy Creek, but their use as prey showed a strong temporal component. Patterns of snail

TABLE 2. FOOD ITEMS OF RIVER DARTERS (*Percina shumardi*) IN THE UPPER BLACK WARRIOR RIVER DRAINAGE, ALABAMA. Relative abundance is the percent occurrence of each prey item among all food items found in all fish stomachs pooled for that date. Sample size for each date is given in Table 1.

Stream	Brushy Creek				Sipsey Fork					
Date	10/27/93	4/15/94	4/14/95	5/16/95	10/28/93	4/14/94	5/10/95	6/13/95	7/19/95	Overall mean
Prey taxa	Mean number of items · fish^{-1} (% relative abundance)									
Crustacea										
Ostracoda	0	0	0.08 (1.3)	0	0	0	0.06 (0.7)	0.03 (0.1)	0.18 (0.3)	0.04 (0.2)
Insecta										
Coleoptera	0	0	0.08 (1.3)	0	0	0	0.19 (2.1)	0.09 (0.3)	0	0.04 (0.2)
Ephemeroptera	0	1.60 (40.0)	0.08 (1.3)	0.20 (1.0)	0	0	0.31 (3.4)	0.47 (1.7)	1.00 (1.8)	0.41 (2.3)
Diptera										
Chironomidae	0	0.80 (20.0)	1.17 (18.7)	9.60 (38.0)	0	0.17 (2.2)	5.63 (62.1)	19.65 (72.3)	2.76 (4.9)	4.42 (24.8)
Tipulidae	0	0	0	0	0	0	0.25 (2.8)	0.09 (0.3)	0.06 (0.1)	0.04 (0.2)
other Diptera	0	0	0	0	0	0	0	0.06 (0.2)	0	<0.01 (<0.1)
Hemiptera	0	0	0	0	0	0	0.06 (0.7)	0.12 (0.4)	0	0.02 (0.1)
Odonata	0	0	0	0	0	0	0.13 (1.4)	0	0.06 (0.1)	0.02 (0.1)
Trichoptera	0	0.60 (15.0)	2.00 (32.0)	15.00 (60.0)	0	0	0.38 (4.1)	0.41 (1.5)	5.18 (9.1)	2.62 (14.7)
Mollusca										
Bivalvia										
Corbicula fluminea	0	0	0	0	0	0	0.44 (4.8)	0.03 (0.1)	0.18 (0.3)	0.07 (0.4)
Gastropoda										
Elimia sp.	12.50 (100)	0.80 (20.0)	2.83 (45.3)	0.40 (2.0)	11.50 (99.5)	7.50 (97.8)	0	5.38 (19.8)	47.35 (83.3)	9.81 (55.1)
Other										
Acari	0	0	0	0	0	0	0.30 (3.0)	0.12 (0.4)	0.06 (0.1)	0.05 (0.3)
Oligochaeta	0	0.20 (5.0)	0	0	0.06 (0.5)	0	0	0.06 (0.2)	0	0.04 (0.2)
fish eggs	0	0	0	0	0	0	1.00 (11.0)	0.06 (0.2)	0	0.12 (0.7)
unidentified invertebrate eggs	0	0	0	0	0	0	0.31 (3.4)	0.53 (1.9)	0	0.09 (0.5)
unknown	0	0	0	0	0	0	0.06 (0.7)	0.03 (0.1)	0	0.01 (<0.1)

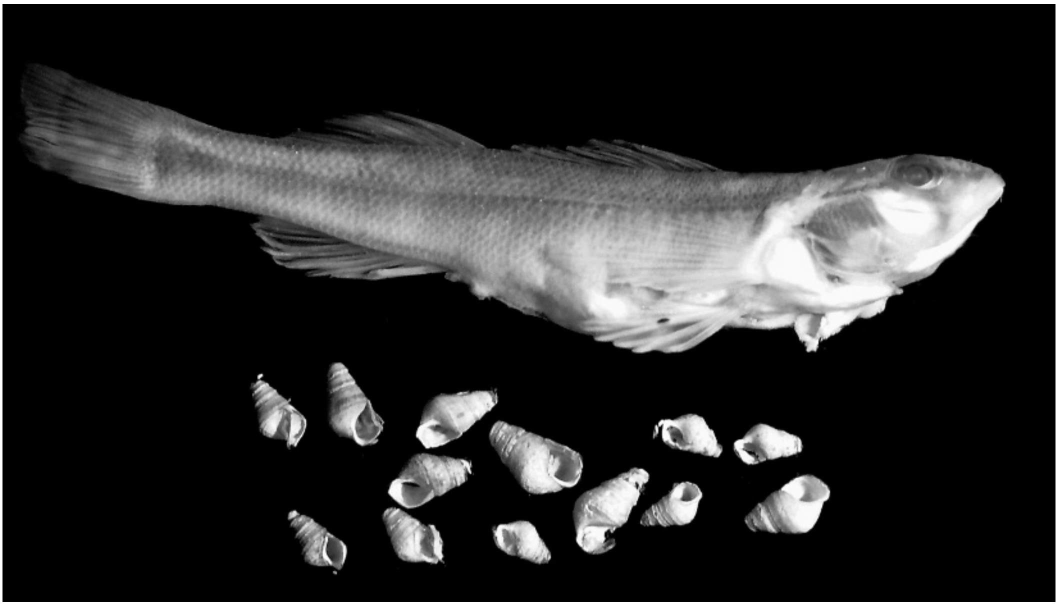

Fig. 1. River Darter (*Percina shumardi*, 58.0 mm SL) from Sipsey Fork Black Warrior River, Alabama, 14 April 1994, showing complete gut contents dissected from the specimen.

use by Snail Darters (*P. tanasi*) in the Little Tennessee River (Starnes, 1977) were similar to those of River Darters in our study. Snails constituted 59% of total Snail Darter food items across the year and ranged from 1–5 mm in width; snail prey was dominated by *Leptoxis subglobosa* (Pleuroceridae) but also included at least six other gastropod species. Snails represented over 90% of food items during winter and fall, but the occurrence of snails in guts dropped to about 40% in spring and summer when caddisfly and dipteran larvae were the predominant prey. Electivity indices suggested snails were selected as prey by Snail Darters, and other prey were consumed opportunistically.

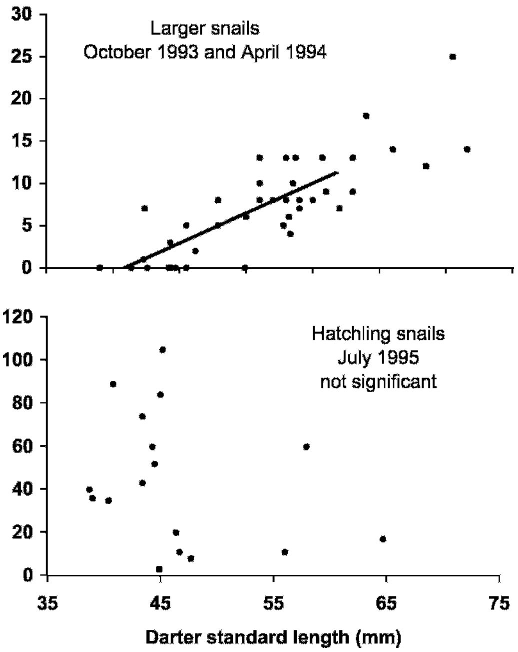

Fig. 2. Number of snails consumed by River Darters during two time periods in the upper Black Warrior River drainage, Alabama.

We did not evaluate prey electivity of River Darters from estimates of prey availability in the study streams. Nevertheless, based on general patterns of stream fish feeding ecology, snail population biology, and prey electivity by Snail Darters and other fishes, we propose two alternative hypotheses that could explain seasonal variation in snail feeding and can serve as a framework for future research on this specialized feeding mode in darters. First, snails may represent suboptimal prey that are used heavily only during periods of scarcity of preferred food items, such as aquatic insect larvae. The period from mid-summer to late fall is generally considered one of food limitation for insectivorous stream fishes, and many fishes exploit alternate prey items or broaden their diet breadth during this time (Angermeier, 1982, 1985; Schlosser and Angermeier, 1990). Under this hypothesis, River Darters may subsist on suboptimal, but abundant larger snails until aquatic insect larvae become abundant in the spring, at which time feeding on larger snails all but ceases. Heavy feeding on hatchling snails occurs in mid-summer perhaps because of easier handling and digestibility of this prey due to their thin shells, but consumption of insect larvae continues during this period, and larger snails remain rare in the diet.

Alternatively, snails may be a preferred food item of River Darters similar to *P. tanasi* (Starnes, 1977). For both species snail growth trajectories and darter gape limitation may intersect to render snails unavailable as a food resource for a short time in late spring. Under this hypothesis, the appearance of hatchling snails in mid-summer signals the beginning of a long period of heavy snail feeding. Heavy snail feeding continues until the following April or May when the previous year's snail cohort grows to a size exceeding the maximum gape of River Darters. The mean maximum snail size consumed by darters in our study was 3.5-mm width and was similar for Snail Darters. Although we did not measure snail abundance and size class structure in our study streams, patterns of pleurocerid snail growth in streams elsewhere in the region show that snails ostensibly harvestable by darters are absent in late spring. In a population of *Pleurocera acuta* in Kentucky and in seven populations of *Elimia* spp. in Alabama, hatchling snails appeared in July, similar to our populations, and by the following April this cohort had grown beyond the mean maximum size of snails harvested by River Darters in our study (Houp, 1970; Huryn et al., 1994). The close correspondence in patterns of snail cohort growth in these studies with the timing of no or lowered snail feeding by River Darters and Snail Darters provides convincing evidence that snails are unavailable as prey items for darters in late spring. In this scenario, darters switch to feeding on insect larvae, a suboptimal prey, only when they cannot feed on snails, their preferred prey. This hypothesis is supported further by studies of other fishes whose optimal prey is snails, for which snails are available as prey only from the time of hatching until they grow to a size exceeding the gape size of the fish (Keast, 1978; Mittelbach, 1984).

Because of the paucity of diet studies for River Darters, we cannot assess the importance of snails as a prey item across the range of this species. The only other record of snail feeding by River Darters is a brief mention of gastropods (no family or species given) found in specimens from the Buffalo River, Tennessee (Starnes, 1977). In the two other published diet studies for River Darters, fish did not eat snails but fed primarily on midge, caddisfly, and mayfly larvae (Thomas, 1970; Sanders and Yoder, 1989), similar to prey items of fish in our study during periods of no snail feeding. However, because both of these studies were restricted to a single sample (summer and early fall), it is unknown if fish in these populations eat snails at other times of the year.

Despite assertions of specialization for snail feeding in all species of *Imostoma* (Etnier and Starnes, 1993), this behavior was well documented previously only for the Snail Darter, *P. tanasi* (Starnes, 1977). The only other published diet study within *Imostoma* is for *P. vigil*, which did not eat snails in spring or fall in the Tombigbee River, Mississippi (Miller, 1983). Similarly, *P. vigil* in the Current River, Arkansas, showed ''virtually no use of snails'' (B. Thompson, pers. comm.). Starnes (1977) mentions snails in guts of *P. vigil*, and Boschung and Mayden (2004) reported the species ''feeds heavily on snails'', but the provenance of these observations is unclear. Other anecdotal observations suggest that *P. uranidea* in the Current River, Arkansas, feeds almost exclusively on snails (B. Thompson, pers. comm.) and that *P. antesella* is ''prone to feed on snails and limpets'' (Etnier and Starnes, 1993). Together with our analyses, these studies suggest that darters in the subgenus *Imostoma*, including River Darters, are at least facultative snail specialists, but it remains unclear to what extent the distribution and abundance of these fishes may be determined by abundance of snail prey.

Apart from *Imostoma*, snails are important food items for few darter species. Although we found records of snail feeding for 18 darter species in addition to members of *Imostoma*, snails represented a minor part of the diet for most species (Table 3). Further, for widespread and well-studied darter species (e.g., *Etheostoma blennioides, E. caeruleum, E. flabellare, E. nigrum*) snail feeding was reported in only a minority of studies, suggesting that snail feeding is not temporally or spatially prevalent for these fishes. Snail feeding by *P. caprodes* was reported in four studies, but snails were a minor component of the diet (Table 3). In an Illinois population of *P. caprodes*, >50% of individuals consumed limpets, but limpets composed only 5–7% of total prey items. Similarly, *P. caprodes* in a West Virginia reservoir consumed snails (*Helisoma* sp.) in every month from May to October with the highest use in June (22% of food items), but overall contribution of snails to the diet was low (2%). In *E. sellare* no snails were eaten in April and May, but snails occurred in 80% of individuals collected in November (mean = 6.2 snails/fish), suggesting that snails are an important component of the diet for this species at least seasonally

TABLE 3. LITERATURE ACCOUNTS OF SNAIL FEEDING BY DARTERS OTHER THAN THE SUBGENUS *Imostoma*. For species with more than one source, gastropod taxa reported in each study, where different, are given in chronological order of the citations.

Darter species	Gastropod taxa eaten	Source
High snail use		
Ethestoma cragini	unidentified	Distler, 1972
E. sellare	*Clappia virginica* (Hydrobiidae)	Knapp, 1976
Low snail use		
Etheostoma aquali	unidentified	R. T. Bryant, pers. comm. in Etnier and Starnes, 1993
E. blennioides	unidentified, *Leptoxis* sp. (Pleuroceridae)	Turner, 1921; Starnes and Starnes, 1985
E. caeruleum	unidentified	Turner, 1921
E. exile	unidentified	Pearse, 1918 in Becker 1983; Turner, 1921
E. flabellare	unidentified	Cahn, 1927; Daiber, 1956
E. fricksium	unidentified	Layman, 1993
E. kennicotti	unidentified	Page, 1975
E. microperca	unidentified	Turner, 1921
E. nigrum	unidentified	Turner, 1921
E. nuchale	unidentified	Howell and Caldwell, 1965
E. olivaceum	unidentified	Page, 1980
E. olmstedi	unidentified	Baker, 1916 in Page, 1983; Sheldon and Meffe, 1993
E. rufilineatum	*Leptoxis* sp. (Pleuroceridae)	Starnes and Starnes, 1985
E. serrifer	unidentified	Jenkins and Burkhead, 1994
E. squamiceps	unidentified	Page, 1974b
E. tuscumbia	Physidae	Koch, 1978 in Etnier and Starnes, 1993
P. caprodes	unidentified, unidentified, *Ferrisia* sp. (Ancylidae), *Helisoma* sp. (Planorbidae)	Turner, 1921; Mullan et al., 1968; Thomas, 1970; Murray and Tarter, 1979
P. evides	*Leptoxis subglobosa* (Pleuroceridae, reported as *Anculosa*)	Starnes, 1977

(Knapp, 1976). Similarly, observations of adult *E. cragini* suggest that snails compose a large portion of the diet of this species as well, but supportive data are lacking (Distler, 1972). Darters are documented to feed on a wide variety of snail taxa, but pleurocerid snails are mentioned specifically as a food item only for *E. blennioides, E. rufilineatum,* and *P. evides* (Table 3).

The rich freshwater fish fauna of eastern North America co-occurs with one of the most diverse freshwater gastropod faunas on Earth (Neves et al., 1997). The snail family Pleuroceridae is particularly diverse and is often abundant in riffle and shoal habitats shared by many species of darters and other fishes. It is therefore surprising that few North American fishes use snails as a major food resource. Even though snails are commonly reported as a minor, perhaps incidental, dietary component for fishes in this fauna (e.g., *Aplodinotus grunniens*, Hoopes, 1960; *Cottus carolinae*, Tumlison and Cline, 2002; *Erimyzon sucetta*, Becker, 1983; *Ictalurus furcatus* and *I. punctatus*, Ross, 2001; Crumpton, 1999), we are aware of only seven species in three families, not including darters, in which snails apparently contribute substantially to the diet. These are the centrarchids, *Lepomis gibbosus* and *L. microlophus* (Huckins, 1997); the catostomids, *Moxostoma carinatum* and *M. lacerum* (Miller and Evans, 1965; Jenkins and Burkhead, 1994); and the ictalurids, *Ameiurus brunneus, A. platycephalus,* and *A. serracanthus* (Yerger and Relyea, 1968). Although the extent of dependence by River Darters on snails remains unknown, River Darters and other *Imostoma* represent some of the few fishes that have evolved to exploit the diverse and abundant pleurocerid snail fauna of eastern North America.

ACKNOWLEDGMENTS

We thank the following people for their various contributions to this study: K. Higgins, L. Page, J. McWhirter, J. Fischer, P. Hartfield, B. Thompson, T. Dell, and B. Kuhajda. Fish used in this study were collected under the State of Alabama, Department of Conservation Permits 93-109, 94-54, and 96-139. Animal care followed ASIH Guidelines for Use of Fishes in Field Research-2004.

Literature Cited

Angermeier, P. L. 1982. Resource seasonality and fish diets in an Illinois stream. Environ. Biol. Fishes 7:251–264.

———. 1985. Spatio-temporal patterns of foraging success for fishes in an Illinois stream. Am. Midl. Nat. 114:342–359.

Baker, F. C. 1916. The relation of mollusks to fish in Oneida Lake. New York State College Forestry, Syracuse Univ., Tech. Publ. No. 4. [not seen]

Becker, G. C. 1983. Fishes of Wisconsin. Univ. of Wisconsin Press, Madison, Wisconsin.

Boschung, H. T., Jr., and R. L. Mayden. 2004. Fishes of Alabama. Smithsonian Books, Washington, D.C.

Burch, J. B. 1982. Freshwater snails (Mollusca: Gastropoda) of North America. EPA-600/3-82-026, Environmental Protection Agency, Environmental Monitoring and Support Laboratory, Cincinnati, Ohio.

Cahn, A. R. 1927. An ecological study of southern Wisconsin fishes. The Brook Silverside (*Labidesthes sicculus*) and the Cisco (*Leucichthyes artedi*) in their relations to the region. Ill. Biol. Monogr. 11:1–151.

Crumpton, J. E. 1999. Relative abundance, age, growth, and food habits of Channel and White Catfish from the Clermont Chain of Lakes, Florida. Amer. Fish. Soc. Symp. 24:115–119.

Daiber, F. C. 1956. A comparative analysis of the winter feeding habits of two benthic stream fishes. Copeia 1956:141–151.

Distler, D. A. 1972. Observations on the reproductive habits of captive *Etheostoma cragini* Gilbert. Southwest. Nat. 16:439–441.

Etnier, D. A., and W. C. Starnes. 1993. The Fishes of Tennessee. Univ. of Tennessee Press, Knoxville, Tennessee.

Haag, W. R., and M. L. Warren, Jr. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. Can. J. Fish. Aquat. Sci. 55:297–306.

Hoopes, D. T. 1960. Utilization of mayflies and caddis flies by some Mississippi River fishes. Trans. Am. Fish. Soc. 89:32–34.

Houp, K. H. 1970. Population dynamics of *Pleurocera acuta* in a central Kentucky limestone stream. Am. Midl. Nat. 83:81–88.

Howell, W. M., and R. D. Caldwell. 1965. *Etheostoma* (*Oligocephalus*) *nuchale*, a new darter from a limestone spring in Alabama. Tulane Stud. Zool. 12:101–108.

Huckins, C. J. F. 1997. Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish. Ecology 78:2401–2414.

Huryn, A. D., J. W. Koebel, and A. C. Benke. 1994. Life history and longevity of the pleurocerid snail *Elimia*: a comparative study of eight populations. J. N. Amer. Bentho. Soc. 13:540–556.

Jenkins, R. E., and N. M. Burkhead. 1994. Freshwater Fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Keast, A. 1978. Feeding interrelations between age-groups of Pumpkinseed (*Lepomis gibbosus*) and comparisons with Bluegill (*L. macrochirus*). J. Fish. Res. Board Canada 35:12–27.

Knapp, L. W. 1976. Redescription, relationships, and status of the Maryland Darter, *Etheostoma sellare* (Radcliffe and Welsh), an endangered species. Proc. Biol. Soc. Wash. 89:99–118.

Koch, L. M. 1978. Aspects of life history of *Etheostoma* (*Psychromaster*) *tuscumbia* in Buffler Spring, Lauderdale County, Alabama. Unpubl. M.S. thesis, Univ.of North Alabama, Florence, Alabama. [not seen]

Layman, S. R. 1993. Life history of the Savannah Darter, *Etheostoma fricksium*, in the Savannah River drainage, South Carolina. Copeia 1993:959–968.

Miller, G. L. 1983. Trophic resource allocation between *Percina sciera* and *P. ouachitae* in the Tombigbee River, Mississippi. Am. Midl. Nat. 110:299–313.

Miller, R. J., and H. E. Evans. 1965. External morphology of the brain and lips in catostomid fishes. Copeia 1965:467–487.

Mittlebach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrachidae). Ecology 65:499–513.

Mullan, J. W., R. L. Applegate, and W. C. Rainwater. 1968. Food of Logperch (*Percina caprodes*), and Brook Silverside (*Labidesthes sicculus*), in a new and old Ozark reservoir. Trans. Am. Fish. Soc. 97:300–305.

Murray, A., and D. Tarter. 1979. Food habitas of the Logperch *Percina caprodes* (Rafinesque), from Easy Lynn Lake, Wayne County, West Virginia. Proc. West Virginia Acad. Sci. 51:73–78.

Near, T. J. 2002. Phylogenetic relationships of *Percina* (Percidae: Etheostomatinae). Copeia 2002:1–14.

Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity, p. 43–86. *In*: Aquatic Fauna in Peril: The Southeastern Perspective. G. W. Benz and D. E. Collins (eds.). Special Publ. 1, Southeast Aquatic Research Institute, Lenz Design and Communication, Decatur, Georgia.

Page, L. M. 1974a. The subgenera of *Percina* (Percidae: Etheostomatini). Copeia 1974:66–86.

———. 1974b. The life history of the Spottail Darter, *Etheostoma squamiceps*, in Big Creek, Illinois, and Ferguson Creek, Kentucky. Ill. Nat. Hist. Surv. Biol. Notes, 89.

———. 1975. The life history of the Stripetail Darter, *Etheostoma kennicotti*, in Big Creek, Illinois. *Ibid.* 93.

———. 1980. The life histories of *Etheostoma olivaceum* and *Etheostoma striatulum*, two species of darters in central Tennessee. *Ibid.* 113.

———. 1983. Handbook of Darters. T.F.H. Publications, Inc. Ltd., Neptune City, New Jersey.

———, and B. M. Burr. 1991. A Field Guide to Freshwater Fishes of North America North of Mexico. Houghton Mifflin, Boston, Massachusetts.

Pearse, A. S. 1918. The food of the shore fishes of certain Wisconsin lakes. Bull. U.S. Bur. Fish. 35:245–292. [not seen]

Ross, S. T. 2001. The Inland Fishes of Mississippi. Univ. Press of Mississippi, Jackson, Mississippi.

SANDERS, R. E., AND C. O. YODER. 1989. Recent collections and food items of River Darters, *Percina shumardi* (Percidae) in the Markland Dam pool of the Ohio River. Ohio J. Sci. 86:33–35.

SCHLOSSER, I. J., AND P. L. ANGERMEIER. 1990. The influence of environmental variability, resource abundance, and predation on juvenile cyprinid and centrarchid fishes. Pol. Arch. Hydrobiol. 37: 265–284.

SHELDON, A. L., AND G. K. MEFFE. 1993. Multivariate analysis of feeding relationships of fishes in blackwater streams. Environ. Biol. Fishes 37: 161–171.

STARNES, L. B., AND W. C. STARNES. 1985. Ecology and life history of the Mountain Madtom, *Noturus eleutherus* (Pisces: Ictaluridae). Am. Midl. Nat. 114:331–341.

STARNES, W. C. 1977. The ecology and life history of the endangered Snail Darter, *Percina* (*Imostoma*) *tanasi* Etnier. Unpubl. Ph.D. diss., Univ. of Tennessee, Knoxville, Tennessee.

THOMAS, D. L. 1970. An ecological study of four darters of the genus *Percina* (Percidae) in the Kaskaskia River, Illinois. Ill. Nat. Hist. Surv. Biol. Notes 70:1–18.

TUMLISON, R., AND G. L. CLINE. 2002. Food habits of the Banded Sculpin (*Cottus carolinae*) in Oklahoma with reference to predation on the Oklahoma salamander (*Eurycea tynerensis*). Proc. Okla. Acad. Sci. 82:111–113.

TURNER, C. L. 1921. Food of the common Ohio darters. Ohio J. Sci. 22:41–62.

YERGER, R. W., AND K. RELYEA. 1968. The flat-headed bullheads (Pisces: Ictaluridae) of the southeastern United States, and a new species of *Ictalurus* from the Gulf of Mexico. Copeia 1968:361–364.

USDA FOREST SERVICE, SOUTHERN RESEARCH STATION, CENTER FOR BOTTOMLAND HARDWOODS RESEARCH, 1000 FRONT STREET, OXFORD, MISSISSIPPI 38655. E-mail: (WRH) whaag@fs.fed.us; and (MLW) mwarren01@fs.fed.us. Send reprint requests to WRH. Submitted: 19 Jan. 2006. Accepted: 18 June 2006. Section editor: C. M. Taylor.